

***A GLOBAL TRAIT-BASED APPROACH TO ESTIMATE LEAF NITROGEN
FUNCTIONAL ALLOCATION FROM OBSERVATIONS***

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1 **A global trait-based approach to estimate leaf nitrogen functional allocation from**
2 **observations**

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Abstract

Nitrogen is one of the most important nutrients for plant growth and a major constituent of proteins that regulate photosynthetic and respiratory processes. However, a comprehensive global analysis of nitrogen allocation in leaves for major processes with respect to different plant functional types is currently lacking. This study integrated observations from global databases with photosynthesis and respiration models to determine plant-functional-type-specific allocation patterns of leaf nitrogen for photosynthesis (Rubisco, electron transport, light absorption) and respiration (growth and maintenance), and by difference from observed total leaf nitrogen, an unexplained “residual” nitrogen pool. Based on our analysis, crops partition the largest fraction of nitrogen to photosynthesis (57%) and respiration (5%) followed by herbaceous plants (44% and 4%). Tropical broadleaf evergreen trees partition the least to photosynthesis (25%) and respiration (2%) followed by needle-leaved evergreen trees (28% and 3%). In trees (especially needle-leaved evergreen and tropical broadleaf evergreen trees) a large fraction (70% and 73% respectively) of nitrogen was not explained by photosynthetic or respiratory functions. Compared to crops and herbaceous plants, this large residual pool is hypothesized to emerge from larger investments in cell wall proteins, lipids, amino acids, nucleic acid, CO₂ fixation proteins (other than Rubisco), secondary compounds, and other proteins. Our estimates are different from previous studies due to differences in methodology and assumptions used in deriving nitrogen allocation estimates. Unlike previous studies, we integrate and infer nitrogen allocation estimates across multiple plant functional types, and report substantial differences in nitrogen allocation across different plant functional types. The resulting pattern of nitrogen allocation provides insights on mechanisms that operate at a cellular scale within leaves, and can be

integrated with ecosystem models to derive emergent properties of ecosystem
productivity at local, regional, and global scales.

Introduction

Nitrogen (N) is one of the important nutrients limiting plant growth (Vitousek and Howarth 1991, Reich et al. 2006, LeBauer and Treseder 2008), yet the representation of this limitation in land models used for climate change prediction is either missing or very uncertain (Zaehle and Dalmonech 2011, Zaehle et al. 2014). Nitrogen limitation increases with increasing latitude because of the less energetically favorable environment for nitrogen fixation (Vitousek and Howarth 1991, Houlton et al. 2008) as supported by analyses in chronosequences (Vitousek et al. 1993, Vitousek and Farrington 1997) and leaf stoichiometry based studies (Reich and Oleksyn 2004). Accurately characterizing plant responses to nitrogen limitation is critical for understanding terrestrial ecosystem responses over the next century, especially in relation to large-scale changes associated with increasing nitrogen deposition (Galloway and Cowling 2002, Matson et al. 2002), release of currently inaccessible soil nitrogen from permafrost degradation due to large-scale warming (Schuur et al. 2007, Natali et al. 2012), and rising atmospheric CO₂ concentrations that increases photosynthetic nitrogen use efficiency and provides a competitive advantage to nitrogen fixers (Ainsworth and Rogers 2007, Rogers et al. 2009).

Predicting plant responses to such large-scale changes requires a mechanistic understanding of nitrogen allocation for different plant processes (i.e., photosynthesis, respiration, growth), and also for cell structure and storage (Xu et al. 2012). Plants allocate nitrogen to produce enzymes and pigments that control these processes at a

cellular scale (Evans 1989, Evans and Poorter 2001). These cellular-scale processes result in emergent local, regional, and global-scale controls on photosynthesis (Ehleringer and Field 1993, Chen et al. 1999, Reich 2012).

At leaf level, the capacity for CO₂ uptake is determined by nitrogen allocated to processes associated with light absorption, electron transport, and carboxylation (Farquhar et al. 1980, Evans 1989, Niinemets and Tenhunen 1997, Evans and Poorter 2001). Nitrogen is used in these processes as proteins to capture light energy in photosystems I/II, to drive the electron transport chain, and as Calvin cycle enzymes. In addition to photosynthesis, the mitochondrial enzymatic reactions that generate adenosine triphosphate (ATP) for maintenance and growth respiration is regulated by nitrogen availability (Wullschleger et al. 1992). Nitrogen is also required for maintaining cell structure and for storage compounds including reproduction and defense (Chapin et al. 1990).

The relative allocation of leaf nitrogen to these component processes and structures has been examined in detail for a few model species (Chapin et al. 1986, Evans 1989, Takashima et al. 2004, Xu et al. 2012) but little is known about how plants in natural ecosystems partition nitrogen resources, especially at regional and global scales. Some global land-surface models represent nitrogen limitation on photosynthesis by down-regulating potential photosynthesis rates if nitrogen is limiting (Oleson et al. 2013), assuming fixed V_{cmax} values for different plant functional types (Moorcroft et al. 2001), predicting V_{cmax} from leaf nitrogen content based on prescribed V_{cmax} -leaf nitrogen relationships (Zaehle and Friend 2010), or accounting for the carbon costs of nitrogen acquisition (Fisher et al. 2010). Although few modeling studies have incorporated

94 varying nitrogen allocation within leaves (Zaehle and Friend 2010), the relationship of
95 nitrogen allocation as a function of leaf nitrogen content is used to predict carbon fluxes
96 which is tuned to match carbon fluxes from flux tower data. In parallel, many studies
97 have shown that plants allocate nitrogen near optimally among leaves across canopy
98 depth (Field 1983, Hirose and Werger 1987, Ellsworth and Reich 1993) and within leaf
99 enzymes (Medlyn 1996, Xu et al. 2012) to maximize productivity given environmental
100 conditions. A mechanistic understanding of nitrogen controls on terrestrial vegetation
101 processes can be improved and parameterized by characterizing leaf nitrogen allocation
102 and how it varies between different plant functional types (PFTs), regionally and
103 globally.

104 Nitrogen allocation in leaves likely varies because defense needs and
105 environmental conditions vary, including carbon dioxide (CO₂), light, and temperature
106 (Evans 1989). Regional differences in nitrogen allocation influence how plants respond to
107 nitrogen deposition, with associated influences on photosynthesis and growth (Reich et
108 al. 2001, Luo et al. 2004, Bobbink et al. 2010). The ability to synthesize regional leaf
109 nitrogen allocation patterns and incorporate them into global land models has been
110 hampered by sparse and isolated measurements of plant traits. Moreover, most global
111 land models have constant photosynthesis parameters (e.g., V_{max}) that control
112 photosynthesis, and nitrogen limitation occurs in these models by down-regulating (e.g.,
113 reducing) potential productivity rather than by dynamically simulating nitrogen allocation
114 parameters based on nitrogen availability (Ghimire et al. 2016).

115 Few observational or modeling-based studies have reported the allocation of leaf
116 nitrogen to a complete set of processes (including carboxylation, electron transport, light

absorption, maintenance respiration, and growth respiration), and those that have focused on relatively few samples. Leaf nitrogen varies with environmental conditions, leaf traits, and geographic location ((Reich et al. 1992, Reich et al. 1997, Reich and Oleksyn 2004, Wright et al. 2004, Wright et al. 2005), and is correlated with photosynthetic parameters (Wullschleger 1993, Xu and Baldocchi 2003, Coste et al. 2005, Grassi et al. 2005). Studies have determined the fractional allocation of leaf nitrogen among proteins and the associated influence on individual process rates (e.g., Evans 1989, Niinemets and Tenhunen 1997, Onoda et al. 2004, Takashima et al. 2004). However these studies relied on a few measurements (i.e., data at only three sites) for evaluating the behavior of their optimal nitrogen allocation model (e.g., Xu et al. 2012), considered limited plant functional types (mostly short-lived non-woody plants or woody juveniles) which lacked explicit representation of inter-species difference in nitrogen allocation (e.g., Chapin et al. 1986, Evans 1989, Makino and Osmond 1991, Onoda et al. 2004, Takashima et al. 2004, Guan and Wen 2011), or did not consider nitrogen allocation for a complete range of processes including carboxylation, light harvesting, bioenergetics, maintenance respiration, and growth respiration (e.g., Coste et al. 2005, Delagrange 2011). Higher nitrogen investments in photosynthesis and respiration are expected for crops followed by herbaceous plants and then longer lived woody plant functional types (Chapin et al. 1986, Evans 1989, Takashima et al. 2004) but the relative magnitudes of the nitrogen partitioning to different functions (especially for tropical and temperate trees) at a global scale is currently lacking. Plants invest the largest proportion of nitrogen for photosynthesis to Rubisco, followed by light absorption and electron transport with allocation sensitive to environmental conditions (Evans and Seemann 1989, Takashima et

al. 2004, Guan and Wen 2011). Compared to photosynthesis, the nitrogen partitioning to respiration is lower (4% to 7%) for crops (Makino and Osmond 1991), but little is known about the respiratory nitrogen allocation for other plant functional types.

In this study, we provide a comprehensive analyses of leaf nitrogen allocation for a range of plant functional types at a global scale by synthesizing observations in the TRY database (Kattge et al. 2011) with observations from a high-latitude Arctic coastal tundra ecosystem (Rogers, unpublished data) (Rogers 2014). We undertake a process-level representation of leaf nitrogen allocation for a range of leaf processes including carboxylation (e.g., Rubisco), light capture, electron transport, maintenance respiration, and growth respiration. We hypothesize that the fractional partitioning of leaf nitrogen to these processes varies with leaf nitrogen content due to changes in plant strategies as leaf nitrogen availability increases. We also estimate how leaf nitrogen allocation varies across a range of plant functional types that have differing photosynthetic nitrogen use efficiency and growth and survival strategies. An important goal of this work is to develop a leaf nitrogen allocation framework that can be integrated into Earth System Models (ESMs) to contribute to a dynamic representation of leaf characteristics. The varying fractional nitrogen allocation within leaves for different processes can be used in ESM's to derive photosynthetic parameters (such as V_{cmax} and J_{max}), leaf pigment content (e.g., chlorophyll), and respiration related parameters.

Materials and Methods

Our goal in this study is to quantify nitrogen allocation in leaves, by combining either observationally inferred (for electron transport rate and Rubisco capacity) or modeled (light capture and respiration) leaf function with the observed stoichiometric

nitrogen ratios required to support that functioning. We also quantify nitrogen allocated to a residual pool, which we assume supports other processes not explicitly represented in this study (e.g., defense). We then assess overall patterns of nitrogen allocation, and compare how nitrogen is allocated to the resolved and unresolved processes.

Plant trait data to quantify nitrogen allocation in leaves were obtained from the TRY and NGEE-Artic databases. The TRY database (Kattge et al. 2011) is a compilation of several original trait databases: this study uses data via TRY from 24 original datasets (Table 1). We have attempted to access as much data as possible from the TRY database based on approval of data providers but note that our sample of data does not represent the entire data available in the TRY database because multiple variables used in this study for the same observational unit are not always available. Our dataset has relatively more samples in mid-latitude and tropical regions compared to high latitude Arctic ecosystems. We therefore additionally acquired data collected by the Next Generation Ecosystem Experiment Arctic (NGEE-Artic) project in Barrow, Alaska that includes data for herbaceous plant functional types in the Arctic.

We integrate observations of leaf nitrogen with photosynthetic and respiratory parameters and rates using a simple model of nitrogen function in leaves to disaggregate the leaf nitrogen into functional pools in different plant functional types. The data used in this analysis are attributed to different plant functional types using the lookup table available from the TRY website (<http://www.try-db.org/TryWeb/Data.php>). In our analysis, nitrogen is allocated to different leaf-level processes: photosynthesis, respiration, and residual (i.e., the remaining leaf nitrogen not allocated to photosynthesis and respiration). Leaf nitrogen allocated to photosynthesis is further divided into light

absorption, electron transport, and Rubisco enzyme. Lastly, leaf nitrogen allocated to respiration is further divided into growth and maintenance respiration. This approach to estimate leaf nitrogen allocated to growth respiration does not explicitly account for leaf age, but the effects of leaf age are implicit in this approach as mature leaves have lower nitrogen, which would reduce gross assimilation and nitrogen allocation for growth, compared to younger leaves in our study. Leaf nitrogen allocated to respiration refers to nitrogen in mitochondrial enzymes associated with mitochondrial respiration for maintenance and growth of plant tissues. We inferred the nitrogen allocation to these processes from the traits (i.e., V_{cmax} , J_{max} , and leaf nitrogen) and used a photosynthesis and respiration model when observations corresponding to certain processes were lacking.

Our approach to partitioning leaf photosynthesis nitrogen to light absorption, electron transport, and Rubisco is based on Niinemets and Tenhunen (1997), and has been used by several studies (e.g., Grassi and Bagnaresi 2001, Le Roux et al. 2001, Walcroft et al. 2002, Han et al. 2003, Ripullone et al. 2003, Coste et al. 2005). Leaf nitrogen partitioning to carboxylation (mainly Rubisco) (P_R) is determined based on the approach by Niinemets and Tenhunen (1997):

$$P_R = \frac{V_{cmax}}{6.22V_{cr}N_a} \quad (1)$$

where V_{cmax} [$\mu\text{mole CO}_2$ (m leaf) $^{-2}$ s $^{-1}$] is the maximum rate of carboxylation by the Rubisco enzyme, V_{cr} [$\mu\text{mole CO}_2$ (g Rubisco) $^{-1}$ s $^{-1}$] is the specific activity of Rubisco, N_a is the leaf nitrogen content [g N (m leaf) $^{-2}$], and 6.22 [g Rubisco (g N in Rubisco) $^{-1}$] converts nitrogen content to protein content (Rogers 2014). At leaf temperature of 25°C, V_{cr} reported in the literature ranges from 20.78 [$\mu\text{mole CO}_2$ (g Rubisco) $^{-1}$ s $^{-1}$] (Niinemets

and Tenhunen 1997) to $47.3 [\mu\text{mole CO}_2 (\text{g Rubisco})^{-1} \text{ s}^{-1}]$ (Rogers 2014), and we estimated the uncertainty in nitrogen allocation for different processes by applying both these V_{cr} values. V_{cmax} is obtained from the maximum rate of carboxylation by the Rubisco enzyme data reported in the TRY database and further standardized to 25°C based on Kattge and Knorr (2007), and N_a is obtained from the leaf nitrogen content $[\text{g N (m leaf)}^{-2}]$ reported in the TRY database.

Leaf nitrogen partitioning to bioenergetics (i.e., electron transport) (P_B) is determined based on the method proposed by Niinemets and Tenhunen (1997):

$$P_B = \frac{J_{max}}{8.06 J_{mc} N_a} \quad (2)$$

where J_{max} $[\mu\text{mole electron (m leaf)}^{-2} \text{ s}^{-1}]$ is the maximum electron transport rate, J_{mc} $[\mu\text{mole electron (}\mu\text{mole cytochrome f)}^{-1} \text{ s}^{-1}]$ is the potential rate of photosynthetic electron transport per unit cytochrome f, and 8.06 $[\mu\text{mole cytochrome f (g N in bioenergetics)}^{-1}]$ converts nitrogen content to protein content (Niinemets and Tenhunen 1997). At leaf temperature of 25°C, J_{mc} equals 156 $[\mu\text{mole electron (}\mu\text{mole cytochrome f)}^{-1} \text{ s}^{-1}]$ (Niinemets and Tenhunen 1997) and J_{max} is obtained from the maximum electron transport rate standardized to 25°C based on Kattge and Knorr (2007).

Leaf nitrogen partitioning to light absorption by chlorophyll (P_L) is determined based on the approach of Niinemets and Tenhunen (1997) and is estimated as:

$$P_L = \frac{C_C}{C_B N_a} \quad (3)$$

where C_C is the chlorophyll content $[\text{mmol chlorophyll (m leaf)}^{-2}]$ and C_B $[\text{1.78 mmol chlorophyll (gN in chlorophyll)}^{-1}]$ is the amount of nitrogen in chlorophyll molecule (i.e., chlorophyll binding coefficient) (Niinemets and Tenhunen 1997). At present, C_C values

are scarce, especially corresponding to data points where V_{cmax} and J_{max} data exist. As a result, we estimate C_c by assuming that plants optimally allocate nitrogen for light absorption and electron transport processes, such that these processes proceed at the same rate (Xu et al. 2012). To assess the uncertainty of this assumption, we consider an additional scenario where these process rates proceed at 80% efficiency, such that the electron transport rate equals 80% of the light absorption rate. The details of the equations used in estimating C_c are provided in Appendix A. Based on the optimal nitrogen allocation assumption, C_c is calculated from the electron transport rate and photosynthetically active radiation (PAR) from a 1 degree spatial resolution 3-hourly surface downward shortwave radiation meteorological forcing dataset (Sheffield et al. 2006) as described in appendix B. We extracted temperature and PAR at each location based on the spatial location of the observations. The uncertainties in nitrogen allocation for efficiency of light absorption and electron transport processes, leaf light exposure, and plant traits are reported as means and standard deviations.

In addition to photosynthesis, leaf respiration is a critical component of plant growth and survival. Nitrogen is used in mitochondrial cellular respiratory enzymes to produce energy (i.e., ATP) by oxidizing the products of photosynthesis (Makino and Osmond 1991). The two major components of respiration are maintenance and growth respiration. Maintenance respiration is associated with a range of processes including protein turnover and synthesis, maintenance of ionic and metabolite gradients, and membrane repair (Ryan 1991a, Amthor 2000). Nitrogen is allocated to mitochondrial enzymes that regulate these processes (Makino and Osmond 1991). Leaf nitrogen partitioning for maintenance respiration (P_M) is estimated as:

$$P_M = \frac{R_M}{R_s N_a} \quad (4)$$

where R_M [$\mu\text{mole CO}_2$ (m leaf) $^{-2}$ s $^{-1}$] is the rate of maintenance respiration and R_s [$\mu\text{mole CO}_2$ (g mitochondrial N) $^{-1}$ s $^{-1}$] is the enzyme activity per unit of mitochondrial protein. At leaf temperature of 25°C, R_s equals 33.69 [$\mu\text{mole CO}_2$ (g mitochondrial N) $^{-1}$ s $^{-1}$] (Makino and Osmond 1991, Xu et al. 2012) and R_M is estimated based on Ryan (1991b) as:

$$R_M = R_b N_a \quad (5)$$

where R_b [0.30 $\mu\text{mole CO}_2$ (gN) $^{-1}$ s $^{-1}$] is the base rate of maintenance respiration per unit nitrogen at 25°C (Ryan 1991b, Oleson et al. 2013).

The second major component of leaf respiration, growth respiration, involves enzyme-mediated growth of new tissues from the photosynthetically fixed carbon, including building tissues involved in photosynthesis, respiration, defense, and cell structure but excluding nitrogen directly invested in regulating these processes. Growth respiration is associated with the metabolic energy used in the construction of organic compounds from substrates (Ryan 1991a). Nitrogen is allocated to mitochondrial enzymes that regulate these processes (Makino and Osmond 1991). Leaf nitrogen partitioning for leaf growth respiration (P_G) is estimated as:

$$P_G = \frac{R_G}{R_s N_a} \quad (6)$$

where R_G [$\mu\text{mole CO}_2$ (m leaf) $^{-2}$ s $^{-1}$] is the rate of growth respiration and R_s [$\mu\text{mole CO}_2$ (g mitochondrial N) $^{-1}$ s $^{-1}$] is the enzyme activity per unit of mitochondrial protein. At a leaf temperature of 25°C, R_s equals 33.69 [$\mu\text{mole CO}_2$ (g mitochondrial N) $^{-1}$ s $^{-1}$] (Makino and Osmond 1991, Xu et al. 2012). This approach to estimate leaf nitrogen allocated to

growth respiration (R_G) does not explicitly account for leaf age (i.e., maturity) (because the TRY database does not explicitly specify leaf age), but the effects of leaf age is implicit in our approach as mature leaves have lower nitrogen, which would reduce gross assimilation and nitrogen allocation for growth, compared to younger leaves in our study. We leave an explicit characterization of the impacts of leaf age on respiration to future work. R_G is determined as a fixed fraction of gross assimilation (Ryan 1991a, b) and is standardized to 25°C based on the temperature response function for respiration as implemented in the Community Land Model version 4.5 (CLM4.5) (Oleson et al. 2013):

$$R_G = f_G f_L A_g \quad (7)$$

where A_g [$\mu\text{mole CO}_2 (\text{m leaf})^{-2} \text{s}^{-1}$] is gross assimilation, f_G (0.25) is the fraction of A_g partitioned to growth respiration (Williams et al. 1987, Ryan 1991b, a), and f_L (0.33) is the fraction of A_g allocated to the leaf (Potter et al. 1993, Malhi et al. 2011). The constant value for fraction of A_g partitioned to growth respiration is consistent with several studies, which have shown that respiration is usually a fixed fraction of productivity (Waring et al. 1998, Gifford 2003, Vicca et al. 2012). A_g is estimated by coupling the Farquhar photosynthesis model with the Ball Berry stomatal conductance model as described in appendix C. Meteorological forcing (i.e., temperature, relative humidity and PAR) for driving the Farquhar photosynthesis model is described in Appendix B.

We assume the remaining leaf nitrogen unallocated to photosynthesis and respiration is allocated as residual nitrogen. Residual nitrogen includes nitrogen used in genetic material (i.e., DNA and RNA), cell structure, defense, and storage for reuse at later time. The residual pool also includes inactive Rubisco, and enzymes other than

Rubisco that are involved in carboxylation. Using the relationships and observations described above, we present the fractional nitrogen allocation for broadleaf deciduous trees, broadleaf evergreen trees, needle-leaved evergreen trees, crops, shrubs, and herbaceous plant functional types.

We provide assessment of the uncertainties associated with trait and climate uncertainties in our nitrogen allocation scheme. As described above, we estimate net carbon assimilation from the Farquhar model (Farquhar et al. 1980) driven separately for two light conditions (low and mean PAR), mean temperature conditions, and mean humidity condition. We considered nitrogen allocation for mean temperature, light, and humidity conditions computed as leaf area index (LAI) weighted daily daytime mean of 1-hourly temperatures, PAR and humidity from 1990 to 2005, respectively. The LAI weighting of temperature, PAR and humidity is performed over each day by weighting the daily daytime mean of 1-hourly temperature, PAR and humidity respectively with the corresponding monthly LAI for the given day. Further details of the calculations of the environmental conditions are provided in the appendix section (Appendix B). In addition to the uncertainty in nitrogen allocation attributed to leaf light exposure, we also report variation in allocation associated with trait variability by bootstrap based sampling (i.e., sampling 75% of the data repeatedly with replacement, and reporting the mean and standard deviation of the repeated samples) of plant traits (e.g., leaf nitrogen and allocation to different processes) rather than using the mean value of plant traits which would ignore the variability within plant functional types. We calculated uncertainties for all the different scenario combinations and then calculated the mean and standard deviation based on these scenario combinations. Furthermore, ANOVA was performed to

test for significant differences in nitrogen allocation amongst different plant functional types and leaf level processes for samples reported in the TRY database for combinations of plant functional types and leaf level processes inferred using mean temperature, light, and relative humidity conditions. The regression slopes and intercepts of the fraction of leaf nitrogen allocation to Rubisco versus leaf nitrogen are derived using the ordinary least squares (OLS) method. However the intercept and slopes of these relationships could be artifacts of the positive intercepts of the V_{cmax} and leaf nitrogen relationship. We therefore also recomputed the slopes and intercepts of these plant functional type dependent relationships by simultaneously fitting to both the V_{cmax} and leaf nitrogen relation (forcing an intercept of zero) as well as the fraction of leaf nitrogen allocation to Rubisco and leaf nitrogen relation using a Bayesian Markov chain Monte Carlo (MCMC) method.

Results

Leaf nitrogen allocation to the different leaf processes varied by PFT (Figure 1), with the error bars representing the standard deviation about the mean. For crops the total nitrogen allocation to the functionally-explained pools (i.e., photosynthesis plus respiration) was 1.61 times larger than nitrogen allocation to the residual pools (which are processes that do not have a clearly defined function in the context of our analysis), primarily because of the large investment in photosynthesis, and 0.93 times larger for herbaceous plants. The total nitrogen allocation to functionally-explained pools relative to residual pools (i.e., ratio of functionally-explained pools to residual pools) are about similar (i.e., 0.80) for broadleaf deciduous trees and non-tropical broadleaf evergreen trees. In the three other plant functional types (shrubs, needle-leaf evergreen trees,

tropical broadleaf evergreen trees), the ratio of total allocation to functionally-explained pools versus the residual pools ranged from 0.70 for shrubs to 0.36 for tropical broadleaf evergreen trees, respectively. Across all plant functional types, the nitrogen allocation to respiration was smaller than the nitrogen allocation to photosynthesis.

For photosynthesis, the largest leaf nitrogen allocation was for Rubisco followed by light absorption and electron transport. The uncertainty in the nitrogen allocation to light absorption is mostly due to trait variations and partly due to uncertainty in the light conditions that leaves were exposed to at the site and that we used in our photosynthesis model. In low light conditions, leaf nitrogen allocation to light absorption is increased in order to capture more light. This increase leads to a corresponding decrease in the nitrogen residual pool, which represents the excess leaf nitrogen after use by photosynthesis and respiration. Conversely, in higher light conditions, leaf nitrogen allocation to light absorption decreased compared to allocation to Rubisco. The total amount of leaf nitrogen allocation to residual and photosynthesis was highest in needle-leaved evergreen trees (predominately found in higher latitudes; Figure 1). This pattern of increasing leaf nitrogen content with increasing distance from the equator has been reported by Reich and Oleksyn (2004).

The patterns of fractional leaf nitrogen allocation to the different processes varied among PFTs (Figure 2) with the ANOVA F-statistic (=107) significantly different (P-value < 0.001). Post hoc tests across combinations of plant functional types and leaf functions showed that the nitrogen fraction allocated to the residual pool was the largest difference amongst different plant functional types followed by nitrogen fraction allocated to Rubisco. In addition, the absolute leaf nitrogen allocation to the different

processes also varied amongst plant functional types with the ANOVA F-statistic (=76) significantly different (P-value <0.001). As expected, crop plant functional types have the greatest fractional leaf nitrogen allocation to photosynthesis (i.e., 8% of leaf nitrogen for electron transport, 29% of leaf nitrogen for Rubisco, 20% of leaf nitrogen for light absorption), consistent with their relatively quick growth rates and genetic modifications to maximize production compared to other nitrogen demands (e.g., defense). The fractional leaf nitrogen allocation to Rubisco, the most important parameter regulating photosynthesis, is lowest in tropical broadleaf evergreen trees (10% of leaf nitrogen).

Leaf nitrogen content was highly correlated with photosynthetic sub-processes and their parameterized representations. V_{cmax} and J_{max} both increased with increases in leaf nitrogen when all plant functional types (PFTs) were grouped together (Figures 3a and 3b). The equations in Figure 3 are determined by forcing the regression through an intercept of zero because if nitrogen is absent, the V_{cmax} and J_{max} values should be zero. This increasing relationship of V_{cmax} and J_{max} with increases in leaf nitrogen has been shown by several studies in individual forest and grassland systems (Wilson et al. 2000, Ripullone et al. 2003, Han et al. 2004, Takashima et al. 2004, Kattge et al. 2009). However, the fraction of leaf nitrogen allocation to Rubisco with increasing leaf nitrogen increased for crops, remained almost unchanged for shrubs (comprised of 79% evergreen and 21% deciduous species) and broadleaf deciduous trees, and decreased for herbaceous plants, broadleaf evergreen trees, and needle-leaved evergreen trees (Figure 4). Nitrogen allocation differences amongst plant functional types and greater variation in the fraction of leaf nitrogen allocation to Rubisco is observed within plant functions types under low leaf nitrogen rather than under high leaf nitrogen conditions. This pattern may reflect

variations due to different plant strategies, nitrogen use efficiencies, and adaptation of species to site-specific environmental conditions (e.g., light, moisture, temperature, and humidity). At high leaf nitrogen there is lower variability, suggesting that most of these plants invest excess nitrogen for functions other than photosynthesis. However we cannot make a conclusive statement of lower variability at high leaf nitrogen because of lower sample size at higher leaf nitrogen compared to lower leaf nitrogen. Future research should investigate differences in nitrogen allocation amongst plant functional types. The recomputed slopes and intercepts determined by MCMC (to minimize the influence of the artifacts of the positive intercepts of the V_{cmax} and leaf nitrogen relationship as described in the materials and methods section) have the same value as the slopes (i.e., 0.07 for crops, -0.07 for herbaceous plants, -0.06 for broadleaf evergreen trees, and -0.04 for needle-leaved evergreen trees) and intercepts (i.e., 0.27 for crops, 0.40 for herbaceous plants, 0.29 for broadleaf evergreen trees, and 0.32 for needle-leaved evergreen trees) determined using OLS (see Figure 4), implying that the slope and intercepts in Figure 4 are not artifacts of the positive intercept of the V_{cmax} and leaf nitrogen relationship. The correlations between fractional leaf nitrogen allocation pools, photosynthesis parameters, and leaf nitrogen for all plant functional types combined are shown in Figure 5. The cluster of positively correlated variables is displayed in blue (bottom half of Figure 5) and the cluster of negatively correlated variables is displayed in brown-red (top of Figure 5).

Discussion

Fractional allocation of leaf nitrogen to various processes (e.g., photosynthesis, respiration, and residual) varies by PFT. In this study, we synthesized leaf nitrogen trait data from the TRY database (Kattge et al. 2011) and a high-latitude Arctic coastal tundra

ecosystem study (Rogers, unpublished data) (Rogers 2014), and integrated these data with a photosynthesis and respiration sub-model. We used the data and model to estimate leaf nitrogen allocation for these various processes at a global scale. The resulting pattern of nitrogen allocation provides insights on mechanisms that operate at a cellular scale within leaves, and can be integrated with ecosystem models to derive emergent properties of ecosystem productivity at local, regional, and global scales. We conclude that existing ecosystem models can be improved by representing each of these processes as functional nitrogen pools within the leaf. The allocation patterns presented in this study can be used to calibrate or evaluate these improved models having functional nitrogen pools. The varying fractional nitrogen allocation within leaves for different processes can be used in ESMs to derive photosynthetic parameters (such as V_{cmax} and J_{max}), leaf pigment content (e.g., chlorophyll), and respiration related parameters. For example, models with a prognostic leaf nitrogen pool (e.g., a version CLM4.5 we developed (Ghimire et al. 2016) can predict variations in photosynthetic parameters with changes in leaf nitrogen. The allocation patterns reported in this study can be used to evaluate models (e.g., OC-N (Zaehle and Friend 2010)) that predict the variation in allocation within leaves.

In our partitioning scheme, the nitrogen partitioning to photosynthesis is lowest in tropical broadleaf evergreen forests (25%) compared to other plant functional types. These tropical trees have low photosynthetic nitrogen use efficiencies (Kattge et al. 2009) and are located on phosphorus-depleted oxisol soils. Therefore, we hypothesize that phosphorous limitation reduces the benefit of larger nitrogen investments to photosynthesis. In contrast, crops have the greatest fractional leaf nitrogen allocation to photosynthesis (57%) (i.e., sum of nitrogen for Rubisco, electron transfer and light

absorption) in comparison to other plant functional types, resulting in higher growth and productivity. Our estimate for crops is comparable to the range of around 50% (shade leaf) to 60% (sun leaf) reported by Evans and Seemann (1989). Takashima et al. (2004) examined evergreen and deciduous species of the genus *Quercus* and found that deciduous species invest higher proportion of leaf nitrogen to photosynthesis (40%) compared to evergreen species (30%), and attributed this difference to greater allocation to cell walls in evergreen species. Although it is difficult to compare directly to Takashima et al. (2004) because our analysis is based on observations for many species, we found similar partitioning to photosynthesis (41% in our study compared to 40%) for deciduous plant functional types (i.e. broadleaf deciduous trees), comparable partitioning (28% and 25% in our study compared to 30%) to photosynthesis for evergreen plant functional types (i.e., needle evergreen trees and tropical broadleaf evergreen trees), and greater allocation to photosynthesis (41% compared to 30%) for non-tropical broadleaf evergreen trees compared to Takashima et al. (2004). A possible interpretation of these results is that the longer leaf longevity of evergreen trees requires a larger fraction of nitrogen to be invested in structural and defensive compounds in order to support the longer-lived leaves.

Across most plant functional types in our study, the largest proportion of nitrogen for photosynthesis is allocated to Rubisco, followed by light absorption and electron transport; these results are consistent with previous studies (Evans and Seemann 1989, Takashima et al. 2004, Guan and Wen 2011). Also, our estimates of the impacts of light levels on nitrogen allocation to light absorption is consistent with several previous studies (Evans 1989, Niinemets et al. 1998), with higher light availability causing reduced

nitrogen investment to light absorption and vice versa. The respiratory mitochondrial protein partitioning of 5% for crops in our study is consistent with the partitioning of 4% to 7% estimated for crops (Makino and Osmond 1991).

The total range of variation for the residual pools across all PFT's considered in this study is around 38% for crops to 73% for tropical broadleaf evergreen trees.

Assuming that respiratory mitochondrial enzymes constitute 5% of total leaf nitrogen, a study by Evans and Seemann (1989) estimated a range of 35% (sun leaf) to 55% (shade leaf) nitrogen partitioning to residual pools for crops, which is comparable to the estimate for crops in our study. Takashima et al. (2004) estimated 55% and 65% nitrogen partitioning (assuming 5% nitrogen partitioning to respiratory mitochondrial enzymes) to residual pools in temperate deciduous and evergreen trees, respectively, which overlaps with our residual pool range of 56% to 73% for tree plant functional types. The large percentage of total leaf nitrogen in the residual pool is hypothesized to be used in structural (cell wall) proteins (6% to 14%; (Takashima et al. 2004, Guan and Wen 2011)), other nitrogen proteins (i.e., proteins not invested in photosynthesis, respiration, and structure; 15% to 25% (after subtracting 5% mitochondrial proteins; (Chapin et al. 1987, Takashima et al. 2004)), free amino acids (2.5%; (Chapin et al. 1987)), lipids (3% to 4% (Chapin et al. 1986)), nucleic acids (8.5% to 15% (Chapin et al. 1986, Chapin 1989, Evans and Seemann 1989)), and CO₂ fixation proteins (other than Rubisco; 4% (Chapin et al. 1987)). In addition, plants produce secondary compounds and metabolites (Bazzaz et al. 1987, Burns et al. 2002, Mithöfer and Boland 2012). Summing these estimates gives 39%-65% nitrogen partitioned to the residual pool, which overlaps but is lower than our estimate of 56% to 73% possibly because our study includes nutrient limited tropical

species having high residual pool sizes. Unlike previous studies that assessed nitrogen allocation for a few plant functional types, our study reported substantial variation in leaf nitrogen allocation amongst different plant functional types. The nitrogen allocations to different processes in this study are correlated to each other because the traits that are used to compute the nitrogen allocations are dependent on each other (e.g., V_{cmax} and J_{max}) (Wullschleger 1993) and also because the nitrogen allocations are dependent on leaf nitrogen content.

In a related study, Xu *et al.* (2012) used a model fitted against a more limited number of site level V_{cmax} data to determine nitrogen allocations for needle-leaved evergreen trees (loblolly pine (*Pinus taeda*)), broadleaf deciduous trees (poplar (*Populus tremula*)), and herbaceous plants (Japanese plantain (*Plantago asiatica*)). However their study reported different magnitudes of nitrogen partitioning compared to our study due to differences in methodology and limited sample size in their study. For example, they reported low nitrogen partitioning to light capture (0.4%-1.4%), and a higher fractional allocation to residual pools for the corresponding deciduous and evergreen plant functional types compared to our estimates and corresponding lower fractional allocation to non-residual pools. These discrepancies are primarily due to their assumptions on the size and turnover time of the storage pool, which we did not include because it is difficult to parameterize. The storage pool used in their study is equivalent to the residual pool in our study (computed as the remaining leaf nitrogen not allocated to the photosynthetic and respiratory functions in our study) with the only difference that the residual pool in our study includes the structural nitrogen pool, which is a separate pool in their study. Finally, in predicting V_{cmax} , they assumed that J_{max} -limited-assimilation balances V_{cmax} -

limited-assimilation, whereas we used estimates for J_{max} and V_{cmax} independently derived from observations.

Our study shows differences across plant functional types (i.e., both increases and decreases) in fractional nitrogen allocation to Rubisco with changes in leaf nitrogen, in contrast to previous studies reporting either an increase or decrease in fractional nitrogen allocation to Rubisco with changes in leaf nitrogen. Our results show an increase in fractional leaf nitrogen allocation to Rubisco with increases in leaf nitrogen for crops, which supports the idea that crops have been selected to maximize productivity at the expense of other possible nitrogen investments, such as defense and structure. Our results are similar to the increase in fractional leaf nitrogen allocation to Rubisco with increases in leaf nitrogen reported by Evans (1989) for crops under carefully controlled conditions. In contrast, we found no change in fractional leaf nitrogen allocation to Rubisco with increase in leaf nitrogen for shrubs and broadleaf deciduous trees, suggesting that these plant functional types allocate the same proportion of nitrogen to Rubisco irrespective of leaf nitrogen content. Furthermore, our results show a decrease in fractional leaf nitrogen allocation to Rubisco with increases in leaf nitrogen content for herbaceous plants, broadleaf evergreen trees, and needle-leaved evergreen trees. These latter results are corroborated by Coste *et al.* (2005), who found a decreasing relationship of fractional leaf nitrogen allocation to Rubisco with increases in leaf nitrogen for several tropical rain forest species. They attributed this decreasing relationship to differences in plant nitrogen use efficiencies and allocation strategies. This decreasing relationship in our study suggests that initial leaf nitrogen is invested in photosynthesis, with further nitrogen allocation to other functions. This decreasing fractional allocation frees up more nitrogen

for the residual pools, which are associated with other functions, including reproduction, defense, structure, hormone production, storage, and reuse at a later time. The fractional leaf nitrogen allocation to residual pool correlates negatively with fractional leaf nitrogen allocation to photosynthetic and respiratory processes. In addition, the fractional leaf nitrogen allocation to electron transport, light absorption and Rubisco are positively correlated with each other.

The fractional leaf nitrogen allocation for different processes was obtained from the TRY database, when possible. When the database lacked a particular trait to derive the fractional nitrogen allocation, we integrated the data with a photosynthesis and respiration sub-model. For instance, leaf nitrogen allocations to Rubisco and electron transport are obtained from measurement based values of V_{cmax} and J_{max} and well-characterized enzyme specific activity rates at standard temperature. Thus we have qualitatively higher confidence in these allocation estimates. This relatively higher confidence on the allocation for Rubisco is important because leaf nitrogen allocation to Rubisco is one of the most important parameters controlling photosynthesis in ecosystem models. Uncertainties in the derived relationships include those resulting from the assumption that Rubisco is fully active (Rogers 2014).

Nitrogen allocation to growth and maintenance respiration are obtained by integrating data and a respiration sub-model. Because this process includes both models and direct measurements, we have lower confidence in the estimated nitrogen demands of respiration. However, the plant respiration models used in this study are effective, simple, and consistent with observations at multiple sites that plant respiration is a fixed fraction of gross productivity (Waring et al. 1998, Gifford 2003, Vicca et al. 2012). The

remaining nitrogen not allocated to photosynthesis and respiration is attributed to the residual pool. Nitrogen allocation within the residual pool varies among different plant functional types. For example, studies have found that nitrogen allocation for defense against biotic and abiotic stressors can vary between plants due to differences in the type, distribution, and amount of defense compounds (e.g., cyanogenic glucosides, glucosinolates, terpenoids, alkaloids, and phenolics) in plants (Bazzaz et al. 1987, Mithöfer and Boland 2012). There is substantial uncertainty in the literature, and no information in the TRY database, regarding how much nitrogen is allocated to individual functions accessing the residual pool, such as defense and hormone production. We therefore identify this lack of information as a critical need for ecosystem models, particularly since the residual nitrogen allocation is a large proportional investment in leaves for some plant functional types, and since allocation of nitrogen to these currently undefined processes may be required to understand tradeoffs associated with different nitrogen allocation strategies.

Conclusions

This study integrated traits derived from observations with a photosynthesis and respiration sub-model to derive global patterns of leaf nitrogen allocation for photosynthesis (Rubisco, electron transport, light absorption), respiration (growth and maintenance), and a residual pool. Across PFTs, the greatest proportion of leaf nitrogen content is allocated to the residual pools, followed by photosynthesis and respiration. Leaf nitrogen allocation to light absorption, a major sub-process of photosynthesis, is strongly controlled by light availability. Based on analysis with the TRY data, tropical broadleaf evergreen trees have relatively low leaf nitrogen allocation to Rubisco. Our

estimates are consistent with several previous studies but also different from some other studies due to differences in methodology and assumptions used in deriving nitrogen allocation estimates. Unlike previous studies, we integrate and infer nitrogen allocation estimates across multiple plant functional types, and report substantial differences in nitrogen allocation across different plant functional types.

Both V_{max} and J_{max} (two key parameters that influence photosynthesis in land models) increase with increases in leaf nitrogen for all PFTs. With increasing leaf nitrogen, the fractional leaf nitrogen allocation to Rubisco (i.e., V_{max}) increases for crops, remains unchanged for shrubs and broadleaf deciduous trees, and decreases for herbaceous plants, broadleaf evergreen trees, and needle-leaved evergreen trees. The increasing relationship suggests that crops invest as much nitrogen as possible for Rubisco to maximize productivity. In contrast, the decreasing relationship for the natural plant functional types implies that as more nitrogen becomes available, a lower proportion is allocated for maintaining higher photosynthetic rates suggesting that if investment in photosynthesis were already optimized, the extra nitrogen would be invested for other functions.

We contend that representation of functional leaf nitrogen allocation in models is important for mechanistic understanding of global change impacts on terrestrial ecosystems, including from nitrogen deposition, changes to soil nitrogen mineralization, and CO₂ fertilization. Our results show systematic patterns that are an advancement for current models, but also show that a large fraction of leaf nitrogen is not explained by our approach, and that a better understanding of the non-photosynthetic and non-respiratory leaf nitrogen requirements—including structural, defensive, and supporting metabolic

functions—may be required to create mechanistic models of leaf nitrogen allocation for natural ecosystems.

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Table 1. References of plant traits used from the TRY database for different plant functional types.

Reference	PFT	V _{cmax}	J _{max}	Leaf N
Harley et al. (1992)	CRP	x	x	x
Unpublished ^a	CRP	x	x	x
Ellsworth et al. (2004)	HRB; SRB; BDT; NET	x	x	x
Meir et al. (2007)	HRB; BDT; BET	x	x	x
Tissue et al. (1995)	HRB	x	x	x
Unpublished ^b	HRB; SRB; BDT; NET	x	x	x
Wohlfahrt et al. (1999)	HRB; SRB	x	x	x
Domingues et al. (2007)	SRB; BET	x		x
Ecocraft Database 1999 (Medlyn and Jarvis 1997)	SRB; BDT; BET; NET	x	x	x
Whitehead et al. (2004)	SRB	x	x	x
Wullschleger (1993)	SRB	x	x	x
Dungan et al. (2003)	BDT; BET	x	x	x
Le Roux et al. (1999)	BDT	x	x	x
Medlyn et al. (1999)	BDT; NET	x		x
Meir et al. (2002)	BDT; BET; NET	x		x
Kattge (2002)	BDT; BET	x	x	x
Ripullone et al. (2003)	BDT	x	x	x
Walcroft et al. (2002)	BDT	x	x	x
Coste et al. (2005)	BET	x	x	x
Domingues et al. (2005)	BET	x		x
Kumagai et al. (2006)	BET	x	x	x
Han et al. (2004)	NET	x	x	x
Tissue et al. (1999)	NET	x	x	x
Walcroft et al. (1997)	NET	x	x	x

^aUwe Grueters PhD dissertation.

^bJens Kattge unpublished data

Abbreviations: CRP=crops; HRB=herbaceous plants; SRB=shrubs; BDT=broadleaf deciduous trees; BET=broadleaf evergreen trees; NET=needle-leaved evergreen trees.

Figures

Figure 1. Inferred leaf nitrogen allocated to maintenance respiration, growth respiration, electron transport, Rubisco, light absorption, and residual in the plant functional types analyzed from the TRY database. The error bars represent standard errors (i.e., the standard deviation about the mean).

Figure 2. Fractional leaf nitrogen allocation for maintenance respiration, growth respiration, electron transport, Rubisco, light absorption, and residual in the plant functional types analyzed from the TRY database. The error bars represent standard errors (i.e., the standard deviation about the mean).

Figure 3. Relationships for all plant functional types between leaf nitrogen content (N) and (a) V_{max25} and (b) J_{max25} . The linear regression equation was fitted with an intercept of 0.

Figure 4. Relationships between leaf nitrogen and the leaf nitrogen fraction allocated to Rubisco for (a) crops, (b) herbaceous plants, (c) shrubs, (d) broadleaf deciduous trees, (e) broadleaf evergreen trees, and (f) needleleaf evergreen trees.

Figure 5. The correlations between fractional leaf nitrogen allocation pools, photosynthesis parameters and leaf nitrogen for all plant functional types combined. In figure caption, *Electron Transport* is fractional leaf nitrogen allocation for electron transport, *Rubisco* is fractional leaf nitrogen allocation for Rubisco, *Light Absorption* is fractional leaf nitrogen allocation for light absorption, *Respiration* is fractional leaf

969 nitrogen allocation for growth and maintenance respiration, *Residual* is remaining
970 fractional leaf nitrogen not allocated to photosynthetic and respiratory processes, *Leaf N*
971 is leaf nitrogen, *V_{cm}25* is the maximum rate of carboxylation by the Rubisco enzyme,
972 and *J_m25* is the maximum electron transport rate.

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Appendix Section

Appendix A. Nitrogen allocation

Chlorophyll content (C_c) and leaf light absorption (e) are related based on the approach by Niinemets and Tenhunen (1997):

$$C_c = \frac{0.076e}{1-e} \quad (A1)$$

where 0.076 is an empirical coefficient [mmol chlorophyll (m leaf)⁻²]. Leaf light absorption (e) is computed as:

$$e = \frac{J_L}{0.292PAR} \quad (A2)$$

where 0.292 is electron to photon ratio [$\mu\text{mole electron } (\mu\text{mole photon})^{-1}$], J_L [$\mu\text{mole electron (m leaf)}^{-2} \text{ s}^{-1}$] is light harvesting rate, and PAR [$\mu\text{mole photon (m leaf)}^{-2} \text{ s}^{-1}$] is photosynthetically active radiation. Light harvesting and maximum electron transport is assumed to occur at 100% efficiency, that is $J_{max}=J_L$ (Xu et al. 2012), and at 80% efficiency, that is $J_{max}=0.8J_L$ at acclimatization temperature. The computation of the photosynthetic acclimatization temperature is outlined in the main manuscript.

Appendix B. Calculation of meteorological drivers for photosynthesis including temperature, PAR and humidity.

We considered nitrogen allocation for mean temperature, light and humidity conditions computed as leaf area index (LAI) weighted daily daytime mean of 1-hourly temperatures, PAR and humidity from 1990 to 2005, respectively. The LAI weighting of temperature, PAR and humidity is performed over each day by weighting the daily daytime mean of 1-hourly temperature, PAR and humidity respectively with the corresponding monthly LAI for the given day. The 1-hourly temperature, PAR and humidity are linearly interpolated from Princeton 3-hourly near-surface temperature, shortwave (assumes 45% of shortwave radiation is PAR (Jacovides et al. 2003)) and humidity respectively. The meteorological

forcing data is weighted with LAI data obtained from the Advanced Very High Resolution Radiometer (AVHRR) sensor (Zhu et al. 2013) because nitrogen allocation occurs during the growing season when plants are photosynthesizing, and by weighting the meteorological forcing data with LAI we are basing the meteorological forcing data on the timing of maximum LAI.

In addition to the mean light condition for photosynthesis, we also calculated a low light condition (equaling 20% of mean PAR). The low and mean light conditions used in this study are assumed to encompass the range of light conditions at the top, and through the vertical profile, of the canopy.

Appendix C. Photosynthesis model

Assimilation is estimated based on the Farquhar model (Farquhar et al. 1980), and is implemented as described in Xu et al. (2012). Net assimilation (A_n) is calculated as a balance of gross assimilation (A_g) and leaf respiration (R_d):

$$A_n = A_g - R_d \quad (C1)$$

A_g is calculated as a minimum of Rubisco limited carboxylation (W_c), and electron transport limited carboxylation (W_j)

$$A_g = \min(W_c, W_j) \quad (C2)$$

W_c is calculated as:

$$W_c = S_c V_{cmaxT} \quad (C3)$$

Where V_{cmaxT} is the maximum rate of Rubisco at temperature (T), and S_c is the V_{cmaxT} scalar multiplier that is dependent on the intercellular carbon dioxide (C_i) concentration. S_c is computed as:

$$S_c = \frac{\max(C_i - C_p, 0)}{C_i + K_{cT}(1 + \frac{O_2}{K_oT})} \quad (C4)$$

where C_p is the light compensation point for CO_2 , K_{cT} is Michaelis-Menten carbon dioxide constant at temperature T , O_2 is internal leaf oxygen partial pressure inside leaf, K_{oT} is oxygen inhibition constant at temperature T .

Electron transport limited carboxylation (W_j) is determined from photosynthetic electron transport (J) as:

$$W_j = S_j J \quad (\text{C5})$$

where S_j is the scalar multiplier for J , and is calculated as:

$$S_j = \frac{\max(C_i - C_p, 0)}{(4C_i + 8C_p)} \quad (\text{C6})$$

J is calculated as:

$$J = J_{maxT} \frac{0.292ePAR}{\sqrt{(J_{maxT}^2 + (0.292ePAR)^2)}} \quad (\text{C7})$$

where J_{maxT} is the maximum electron transport rate at temperature (T), e is leaf light absorption, and PAR is photosynthetically active radiation.

Leaf respiration (R_d) is computed as a fraction of V_{cmaxT} :

$$R_d = 0.015V_{cmaxT} \quad (\text{C8})$$

Photosynthesis is coupled to stomatal conductance (g_s) using the Ball Berry type equation (Ball et al. 1987, Collatz et al. 1991).

$$g_s = m \frac{A_n}{C_s} h_s p + b \quad (\text{C9})$$

where h_s is surface relative humidity, p is atmospheric pressure, C_s is surface carbon dioxide concentration, and m and b are the slopes and intercepts of the Ball Berry equation.

Intercellular carbon dioxide concentration (C_i) is computed from a Fickian diffusion equation:

$$C_i = C_s - \frac{1.6A_n}{g_s}p \quad (\text{C10})$$

These photosynthesis equations are solved iteratively with an initial guess of c_i , followed by computing A_n based on the Farquhar model, determining Ball-Berry g_s , recalculating c_i based on Fickian diffusion, and then repeating the calculations with the new c_i .

Supplementary Information

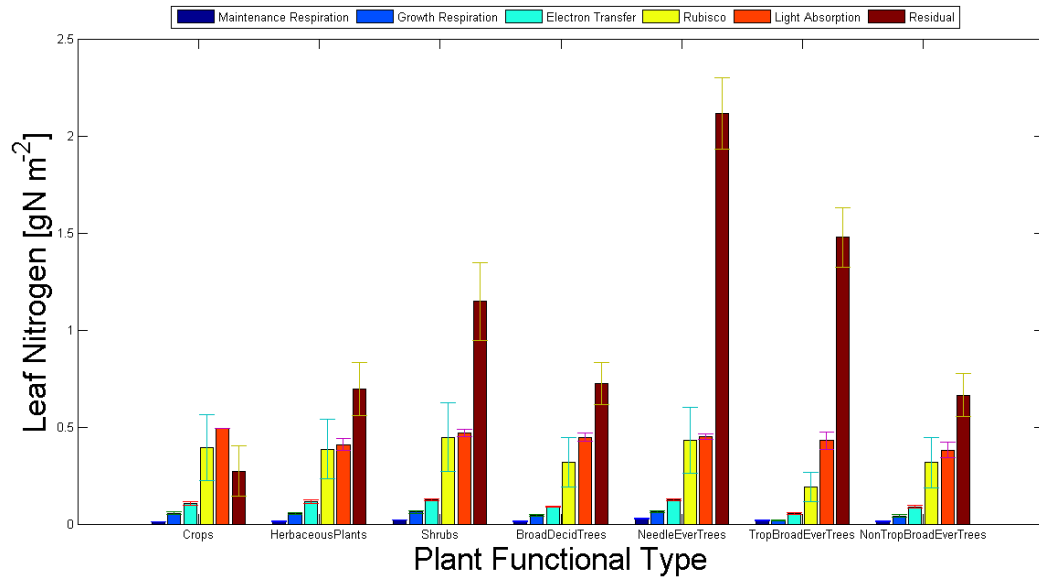


Figure S1. Inferred leaf nitrogen allocated to maintenance respiration, growth respiration, electron transport, Rubisco, light absorption, and residual in the plant functional types analyzed from the TRY database assuming low light conditions. The error bars represent standard errors (i.e., the standard deviation about the mean).

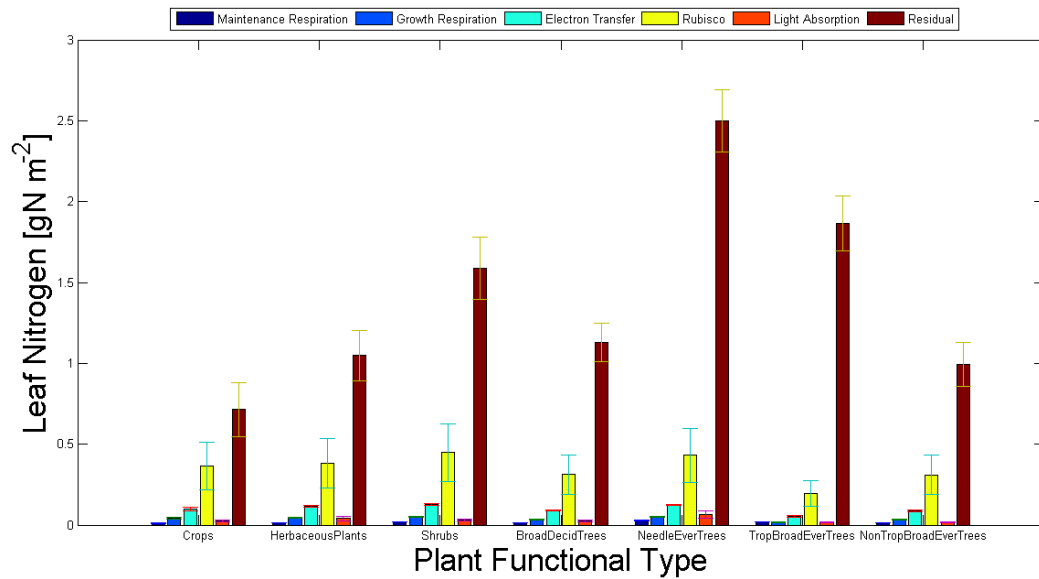


Figure S2. Inferred leaf nitrogen allocated to maintenance respiration, growth respiration, electron transport, Rubisco, light absorption, and residual in the plant functional types analyzed from the TRY database assuming mean light conditions. The error bars represent standard errors (i.e., the standard deviation about the mean).